SCIENTIFIC PAPERS.

THE FLORIDA STRANGLING FIGS.

BY ERNST A. BESSEY.

The genus *Ficus*, in particular the section *Urostigma*, contains many species that have, in their earlier stages, a tendency to assume the epiphytic habit. This is the case, according to Engler,* with *F. elastica* Roxb., *F. bengalensis* L., less often with *F. infectoria* Roxb. and still more rarely with *F. religiosa* L. In Mexico, as described by Trelease,† a species doubtfully referred to *F. ligustrina* K. & B., but, as Dr. Trelease informs me, held by Warburg to be rather *F. radula* or a closely allied undescribed species, is abundant as an epiphyte upon *Sabal mexicana*, the plants becoming eventually self-supporting on their trunk-like roots.

There are two native species of figs in Florida: *F. aurea* Nutt. and *F. populnea* Willd. Under circumstances both may exhibit the epiphytic habit when young, although the latter species shows the characteristic only rarely. So far the writer has observed it as an epiphyte only once, upon *Quercus virginiana* Mill. He has observed *F. aurea* upon the following trees, the first two being the most common hosts: *Quercus virginiana* Mill. (plate 1), *Sabal palmetto* (Walt.) R. & S. (plate 2), *Metopium metopium* (L.) Small (plate 4, fig. 1), *Bursera simaruba* (L.) Sarg., *Coccolobis laurifolia* Jacq., *Gymnanthes lucida* Sw. (plate 5, fig. 1), *Dipholis salicifolia* (L.) A. D. C., and even on large trees of its own species (plate 4,

* Engler & Prantl. Die natürlichen Pflanzenfamilien. III. 1: 89-92. (1888).

† Trelease, Wm. Illustrations of a "Strangling" Fig Tree. Sixteenth Annual Report of the Missouri Botanical Garden. 161-165. Pls. 34-45. (1905).

fig. 2). In dense hammocks *F. aurea* seems to grow only as an epiphyte at the start, although eventually all trace of this habit is lost. In open places, however, it is often independent from the first (plate 3). It is often set out as a street or yard tree in Miami (plate 5, fig. 2). Such trees have a single upright true trunk and rounded head, and are rather ornamental at first. Eventually, however, they begin to send down rootlets from their branches. These, upon taking root, enlarge rapidly, so that the local name for the tree, wild banyan, is not at all inappropriate. The trees that start epiphytically usually arise from seeds that lodge in knotholes (plate 4, fig. 1) or crotches of branches, or the axils of the palmetto leaves, probably through the agency of birds, as these are very fond of the fruits. The young seedlings grow slowly at first. Soon the roots begin to elongate rapidly, remaining of small diameter and growing downward in close contact with the bark or even swinging loosely. Only when the roots have established connection with the ground does the growth of the plant become rapid. The roots then increase in thickness very rapidly and new roots are sent down. These anastomose wherever they come into contact, forming a close network around the trunk of the doomed supporting tree. Soon the thickening roots close up all the holes, making a firm tube enclosing the trunk of the host and killing it very soon by preventing growth in thickness, *i.e.* practically girdling it for a long distance up and down the trunk. The palmetto is an exception, however, for, since the stem does not increase in thickness, it suffers no immediate inconvenience and may remain alive for years after its trunk is firmly encased by the fused roots. Eventually, however, it will be so overtopped and shaded by the *Ficus* that it dies, but this may not be for many years. In old age a tree of *Ficus aurea* will have many root trunks and may have a spread of 25 meters or even more, and a height of over 15 meters.

Both *F. aurea* and *F. populnea* have two or more crops of fruits in a year. In the former species the receptacles are sessile, in pairs in the leaf axils (plate 6), in the latter they are long stalked, single or in pairs (plate 7). Both species belong to the section *Urostigma*, and have staminate and seed

and gall producing pistillate flowers in the same receptacle, the receptacle being axillary to the smooth, entire leaves. The staminate flowers have but one stamen. Each flower is subtended by a small bract while several rows of bracts surround the opening of the receptacle. The staminate flowers are scattered among the others and do not come to maturity until the fruit is ripe. Pollination is accomplished by species of *Blastophaga*, different in the two figs. These reach maturity with the seeds at the time that the receptacle is about to begin to ripen pomologically. Just at this time the staminate flowers reach maturity so that the pollen is shed while the insects are emerging from the galls. The fecundated females become covered with pollen in their search for the point of exit from the mature receptacle. They seek out the young receptacles in which the pistillate flowers are just ready for pollination. Usually but one, occasionally two insects enter a receptacle, losing their wings as they force their way between the outer scales which surround the opening. These scales are appressed tightly in several series but loosen up at the time when the flowers are ready for pollination, permitting the *Blastophaga* to force her way between them with not too much difficulty. As the insect works around over the flowers in the act of depositing her eggs she leaves on the receptive stigmas the pollen adhering to the hairs that cover her body and appendages. But one egg is laid in each flower, the ovipositor apparently being inserted down the hollow of the style, the egg being placed in the upper part of the ovary upon the top of the ovule, where it was observed in several cases. Counts were made in several mature receptacles of both species to determine the number of flowers in which *Blastophaga* larvae developed and of those developing seeds. This is shown in the accompanying tables:

TABLE A.

No.	Seed flowers.	Gall flowers.	Per cent. female flowers with galls.	Staminate flowers.	Per cent. staminate among all flowers.
1	125	103	45	.....	.....
2	112	117	51	.....	.....
3	79	104	57	.....	.....
4	39	101	72	21	13
5	45	87	66	14	8.4

FICUS AUREA.

TABLE B.

No.	Seed flowers.	Gall flowers.	Per cent. female flowers with galls.	Staminate flowers.	Per cent. staminate among all flowers.
1	148	230	66	54	12.5
2	114	247	68	73	17

FICUS POPULNEA.

In many species of *Ficus* there are two types of pistillate flowers, one producing seeds, the so-called seed flowers, and the other present only to receive the *Blastophaga* eggs, one in each flower, producing the *Blastophaga* galls, the so-called gall flowers. These gall flowers require the stimulus of the egg to cause them to develop further. Otherwise they degenerate, as they are incapable of producing seeds. Careful study of the flowers shows that this distinction does not exist in the species under consideration. It is indeed a fact that two extremes of the pistillate flowers may be distinguished—those with long and those with short styles (plate 8, figs. 1-3, *F. aurea;* 8-9, *F. populnea*). This is correlated with the length of the flower pedicel so that all the stigmas occupy the same level. The difference in length of the pedicels seems to be an arrangement permitting the flowers to be present in two layers instead of in merely one. There are many intergradations, however, between the two extremes (plate 8, fig. 2).

It is a fact that the long-stalked, short-styled flowers are preferred by the ovipositing *Blastophaga*, for only rarely can one find more than one or two such flowers producing seeds, they being usually occupied by *Blastophaga* larvae (plate 8, fig. 7). However the fact that such flowers of this type as escape oviposition do develop perfect seeds demonstrates that they are not specialized gall flowers. Furthermore, of the short-stalked, long-styled flowers always a certain proportion, varying from 5 to 20 per cent., contain *Blastophaga* larvae, yet there are no observable differences in this type of flowers at the time of pollination.

The single stamen is plainly divided into filament and anther in *Ficus populnea* (plate 8, fig. 10), and is larger than that of *F. aurea* in which the anther cells lie upon the top of a somewhat obliquely truncate column (plate 8, figs. 4-6). The calyx lobes in both staminate and pistillate flowers are smaller proportionally and more distinct in *F. aurea*. They are mostly three in number in both kinds of flowers. In *F. populnea*, at least in the specimens studied, the calyx lobes seem to be two in number in the pistillate flowers, and come well up above the top of the ovary. Possibly the larger lobe represents in reality a union of two. In the staminate flowers but one large lobe could be found. Whether it represents a union of several lobes or not was not determined. In both species the ripe achenes have an outer layer of cells that form mucilage in water. On drying, this serves to glue the achenes in place.

A study of the germination of the seeds of *Ficus aurea* revealed the very interesting fact that it is dependent upon light, not taking place if the achenes are left dark. The following experiments were performed in this connection:

October 22, 1907, several ripe fruits were opened and the achenes and surrounding pulp together with empty galls were placed in two Petri dishes upon filter paper moistened with Knop's mineral nutrient solution. One dish was placed on a table next to a north window, the other in the back of a long drawer in the same table. In the former the first signs of germination were observed November 1 and by November 6 apparently all the seeds had germinated. In the dark there

was no germination at this date. The dish was then placed in the light and in two days one seed, and in a week all the seeds, had germinated.

November 5 the achenes were carefully washed out of the pulp of some more fruits and thirty-three placed as above on filter paper in each of two dishes, one dish being placed in the dark as before. November 12 twelve of the seeds in the light showed germination while all thirty-three had germinated by the 16th (plate 9). On the 21st none of the seeds in the dark showing any signs of germination ten were transferred to the light to test whether they were still alive. In twenty-four hours one germinated, three days later five others split their seed coats, while eight days after the transfer to the light all had germinated. Five more seeds transferred to the light December 7 had begun to germinate by the 13th. Five more were transferred to the light December 21. On returning January 2 after a few days' absence they were all found to have germinated. January 7 none of the thirteen seeds still remaining in the dark had germinated. The whole dish was accordingly transferred to the light. The seeds, unfortunately, were allowed to dry out about January 1 and again January 12. On January 17th three seeds showed germination while in two or three others the seed-coats were beginning to split, showing that while the vitality had been apparently somewhat reduced the seeds were still capable of responding to the stimulus afforded by the light. By January 20 all the remaining seeds had germinated.

In a third experiment the achenes were washed free from empty galls and pulp and poured in water upon the surface of the soil in three pots, two being kept in a dark cupboard and one on a porch exposed to the sun in the early morning. In the latter, the seeds germinated in nine days while in the dark there was no germination in one pot after more than sixty days. After twenty-seven days the other pot was placed on the porch and germination was first noticed in thirteen days. In watering, the achenes had been partly covered with a thin layer of soil which perhaps explains why the germination was delayed until thirteen days had elapsed.

Similar experiments in Petri dishes with achenes of *Ficus populnea* showed a less marked light requirement for germination. On November 21 the seeds were sown, fifteen in each dish. On November 27 seven showed the beginning of germination in the dish in the light while by December 3 all fifteen had germinated. Not until December 6 did the first seed germinate in the dark, followed by one each on the 9th, 13th and 14th, three on the 16th, one on the 21st and one more by the 26th. The remaining six seeds not having germinated by January 7, the whole dish was placed in the light. Ten days later one seed had germinated while four more germinated by the 25th, the last seed germinating about February 1. It is probable that in this experiment the drawer in which the seeds were kept dark was not absolutely dark, as the cotyledons of the plantlets produced showed a very faint greenish tinge. The plants were extremely elongated, however, showing a great light deficiency. The conditions, however, were similar to those under which *F. aurea* refused to germinate.

The light requirement for germination on the part of *Ficus aurea* evidently stands in the closest relation to its mode of life and explains why the epiphytic habit is the only one assumed in the dense hammocks. As was mentioned before, the trees of *F. aurea* occurring in dense woods pass their early life as epiphytes. It is only in natural or artificial clearings, along rocky bluffs (plate 3) or canal banks, etc., where the shade is not too dense, that one finds young *F. aurea* not epiphytic. In the uncut hammocks the light even at midday resembles twilight in the open. On the ground under the shrubs and herbaceous undergrowth and covered by the constantly falling leaves it is evident that the seeds of *Ficus aurea* would be unable to germinate although they might obtain enough light for this purpose in a clearing or on a rocky bluff. So it is that in the hammocks only those seeds germinate that have been deposited in the tops of trees where they can obtain sufficient light. As is naturally to be expected, even in clearings and open places *Ficus aurea* will be found as an epiphyte as well as growing independently. In the case of *F. populnea* this lack of light doubtless has

some effect, but from the results of the experiment it is evident that but little light if any is necessary to cause some at least of the seeds to germinate. This, in the writer's opinion, is the explanation of the presence of this tree as a hammock inhabitant, without assuming the epiphyte habit.

There are but few plants known the seeds of which possess the peculiarity described above for *Ficus aurea*. Pfeffer* refers to Wiesner's† observation that the seeds of *Viscum album*, likewise epiphytic in habit, require light for their germination although this does not hold true for tropical species of *Viscum* nor for *Loranthus europaeus*. For the tropical *Viscum* species germination is favored by light although it is not necessary. In a footnote Pfeffer notes that Raciborski claims that light is requisite for the germination of *Nicotiana*. It is of interest that, while in *Viscum album* light is essential for germination of a seed, the seedling thus produced turns away from the light. This is not the case with either *Ficus aurea* or *F. populnea*, for their seedlings are very positively heliotropic. The roots, on the other hand, are rather distinctly negatively heliotropic. Both features are shown fairly well in plate 9 for *F. aurea*. In this respect these species are not confirmatory of Davenport's‡ conclusion that the inability of *Viscum album* to grow or germinate in the dark is correlated with the peculiarity in its phototropic response that the hypocotyl turns away from the light.

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* Pfeffer, W. Pflanzenphysiologie. II Auflage. **2**: 105. (1904).

† Wiesner, J. Ueber die Ruheperiode und über einige Keimungsbedingungen der Samen von *Viscum album*. (Ber. Deutsch. Bot. Gesell. **15**[10]: 503–516. 1898).

‡ Davenport. Experimental Morphology. Part II. 423 and 438.

EXPLANATION OF PLATES.

All the photographs were made by the author except plates 6, 7 and 9 which were made by Mr. G. L. Fawcett. They were all taken in the vicinity of Miami, Florida, in the autumn and winter of 1907.

Plate 1.—*Ficus aurea* on *Quercus virginiana.*

Plate 2.—Young plant of *Ficus aurea* on *Sabal palmetto.*

Plate 3.—*Ficus aurea* growing non-epiphytically on a rocky ledge.

Plate 4.—1, Young seedling of *Ficus aurea* growing in a hole in the trunk of *Metopium metopium.* 2, *Ficus aurea* growing epiphytically on a dead trunk of *F. aurea.*

Plate 5.—1, *Ficus aurea* upon trunk of *Gymnanthes lucida* which it has killed. 2, *Ficus aurea* about twenty-five years old, planted as a yard tree.

Plate 6.—Fruiting branch of *Ficus aurea,* one-fourth natural size.

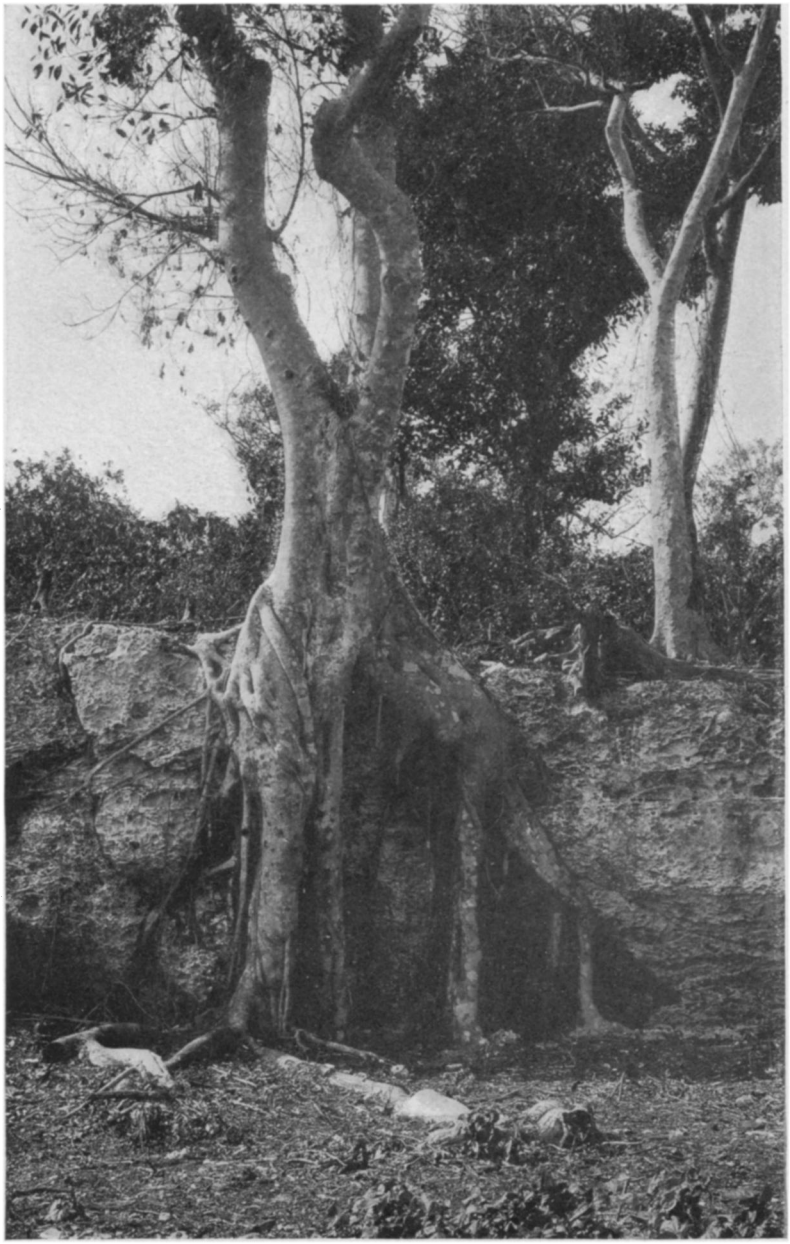
Plate 7.—Fruiting branches of *Ficus populnea,* three-eighths natural size.

Plate 8.—1-3, Pistillate flowers of *Ficus aurea* from a receptacle into which a *Blastophaga* had just entered, all magnified about 100 times. 4-5, Staminate flowers of *Ficus aurea* magnified about 35 times. 6, Top view of stamen of *Ficus aurea,* magnified about forty times. 7, *Blastophaga* gall of *Ficus aurea* from which the insect has just escaped, magnified about 25 times. 8-9, Pistillate flowers of *Ficus populnea* ready for pollination, magnified about 24 times. 10, Staminate flower of *Ficus populnea,* magnified about 24 times. All drawn with the aid of camera lucida.

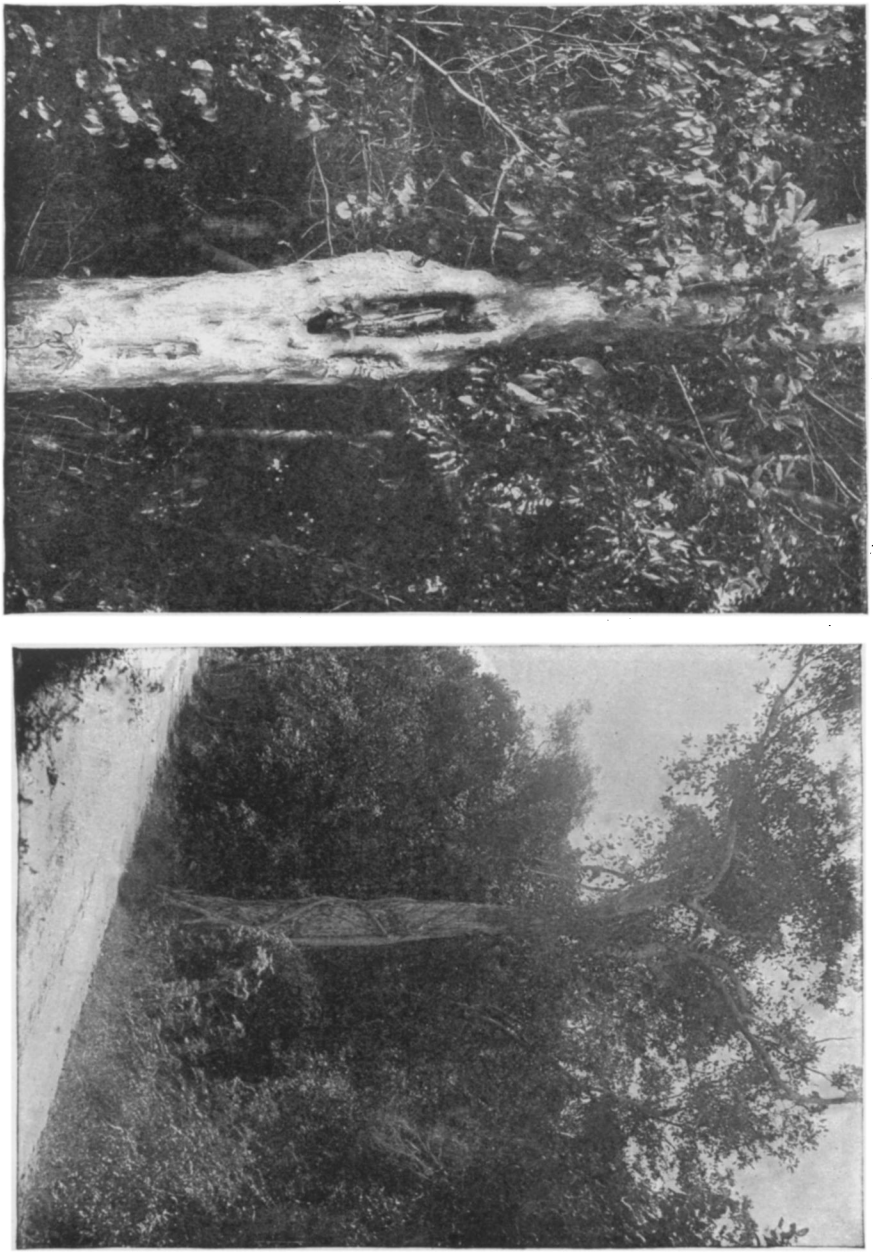
Plate 9.—Germination of *Ficus aurea* in light and in dark. The Petri dish showing the little seedlings was exposed to the light. The positive heliotropism of the hypocotyls and the quite marked negative heliotropism of the roots is shown.

FICUS AUREA ON QUERCUS VIRGINIANA.

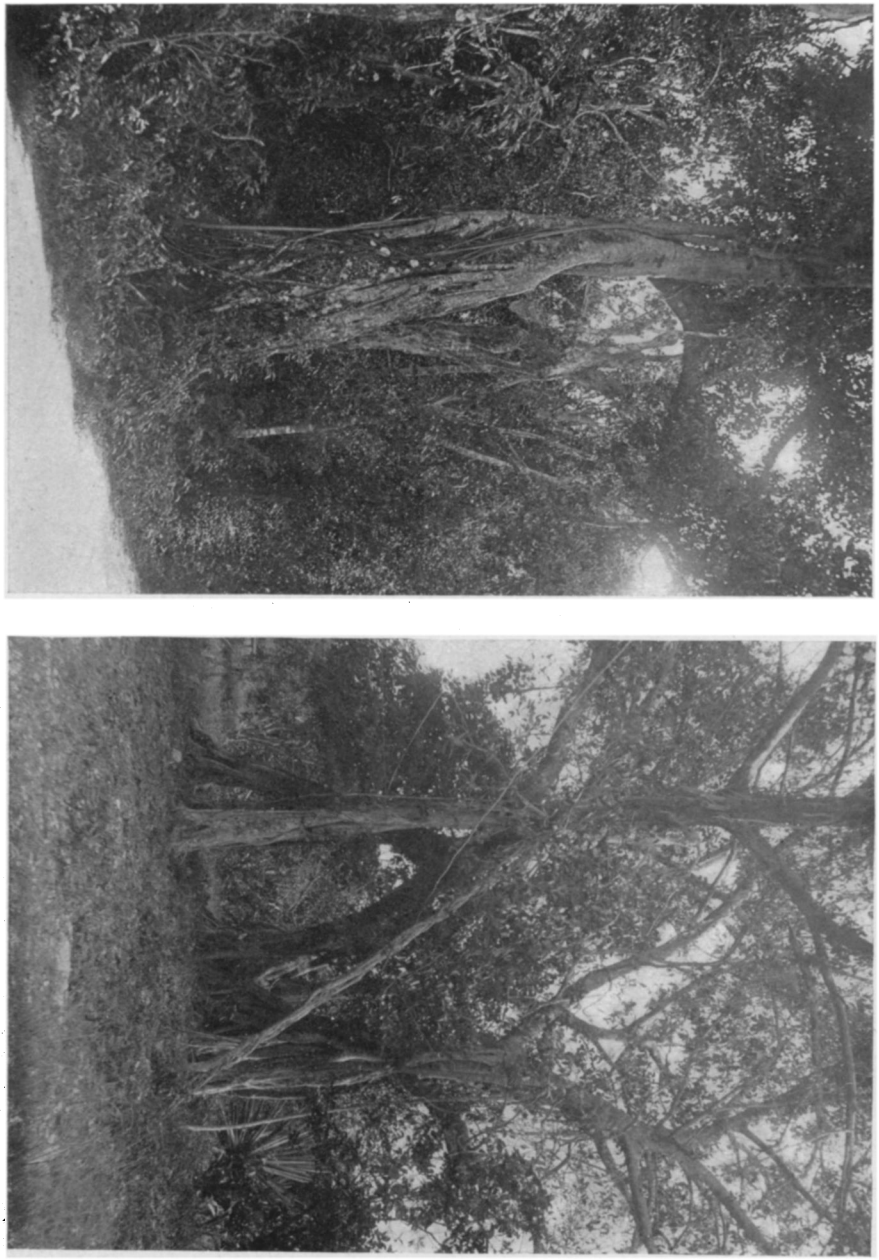
FICUS AUREA ON SABAL PALMETTO.



FICUS AUREA

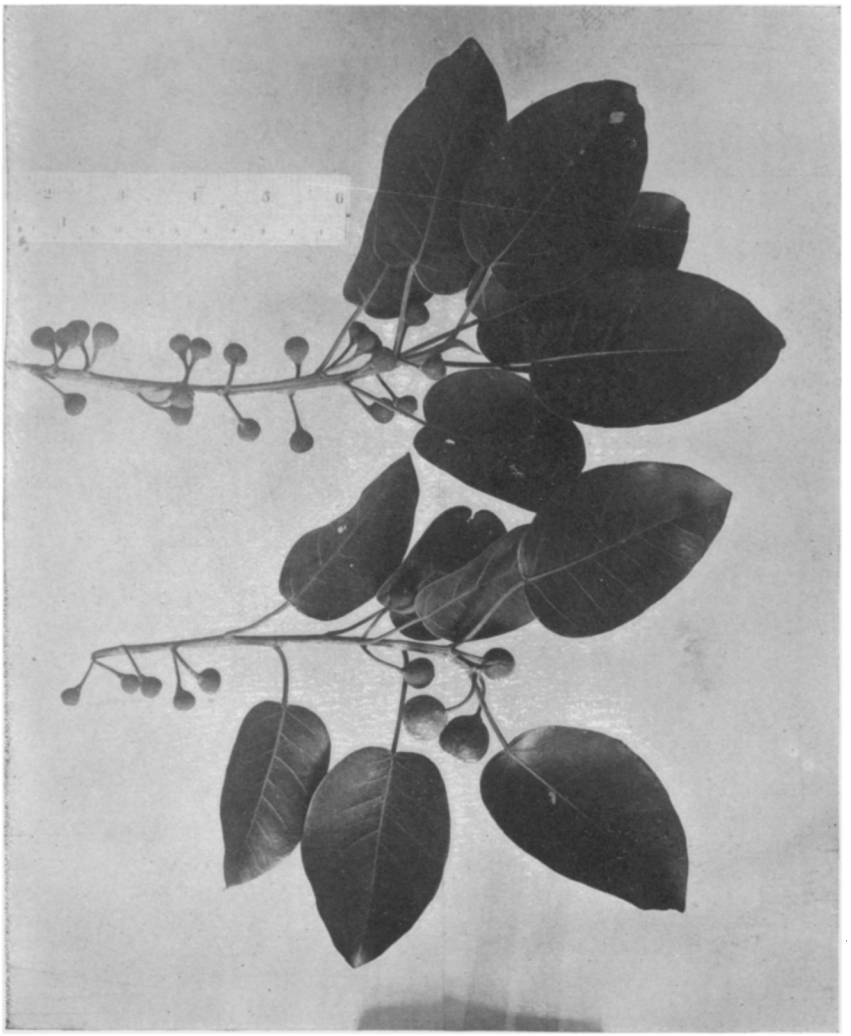


FICUS AUREA.

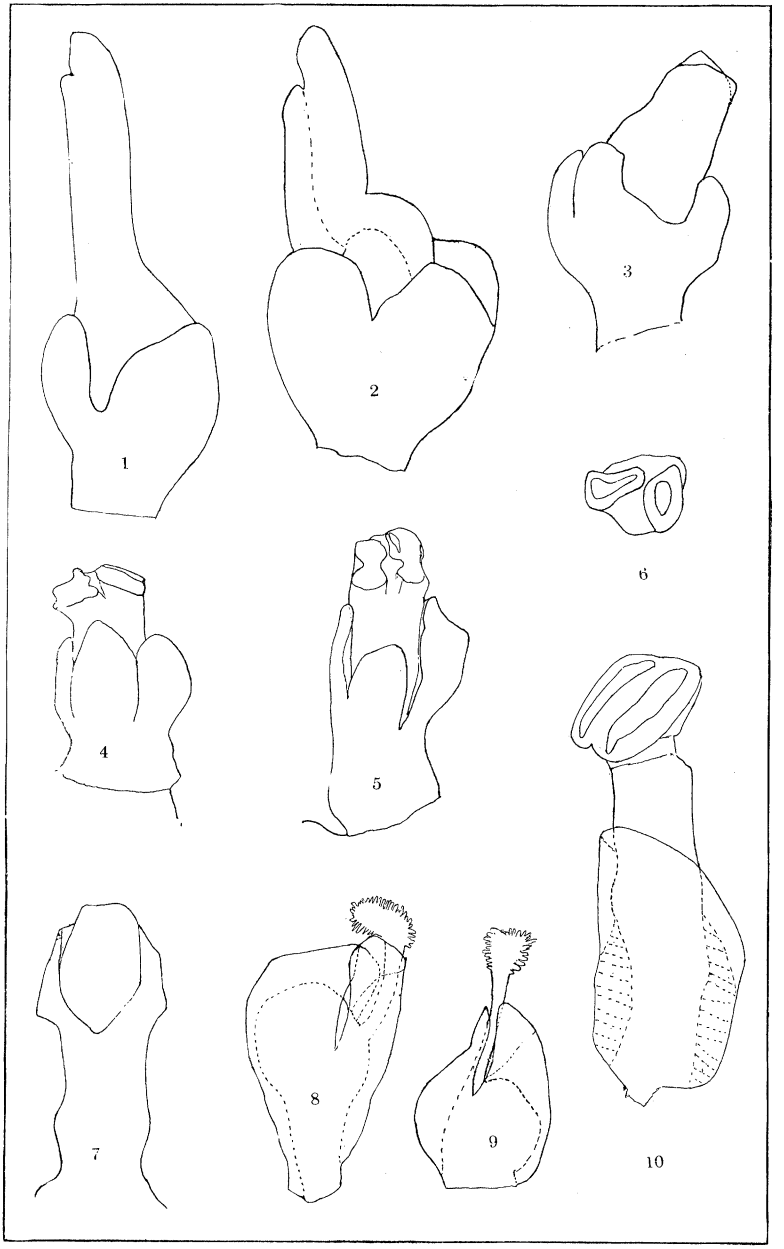


FICUS AUREA.

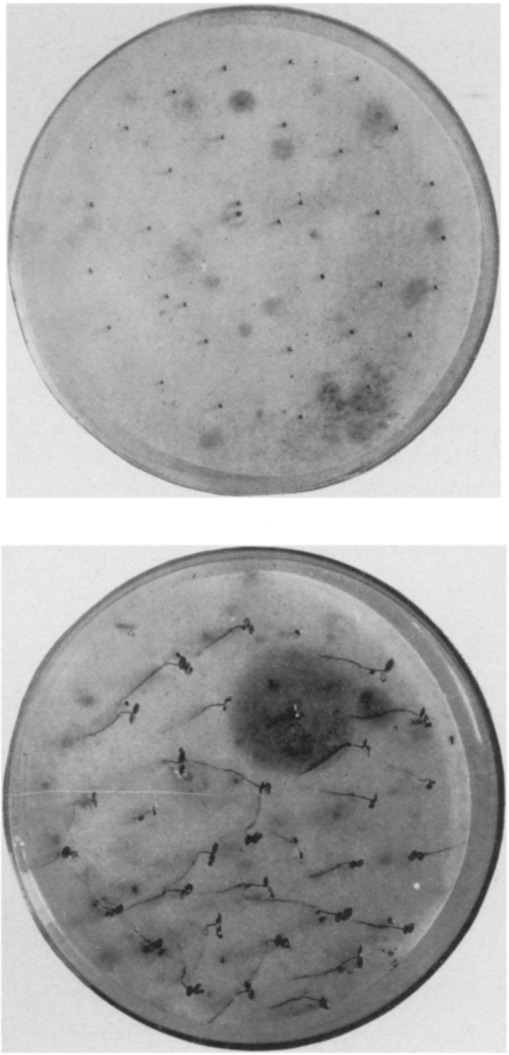
FICUS AUREA.



FICUS POPULNEA.



FICUS AUREA AND F. POPULNEA.



GERMINATION OF FICUS AUREA.